GERMINATION IN THE WESTERN AUSTRALIAN PITCHER PLANT *CEPHALOTUS FOLLICULARIS* AND ITS UNUSUAL EARLY SEEDLING DEVELOPMENT

By JOHN G. CONRAN
Department of Botany, The University of Adelaide, SA 5005

and MATTHEW D. DENTON
Department of Agronomy and Farming Systems,
The University of Adelaide, Roseworthy Campus, SA 5371

ABSTRACT

The pattern of germination and seedling morphology of *Cephalotus follicularis* are reported in detail for the first time. Germination is epigeal phanerocotylar, with the first leaves alternate. The testa is carried out of the fruit on the apex of a cotyledon, but the seedlings develop an expanded but non-vascularized extension of the hypocotyl. This grows back into the remnant carpel (follicle), filling it and possibly acting as a (non-starchy) food reserve for the young seedling. However, this utilisation of the follicle might also act to protect the seedling both from invertebrate herbivores and from dehydration, absorbing water through capillary action.

INTRODUCTION

The Cephalotaceae are an unusual carnivorous pitcher plant family consisting of a single species *Cephalotus follicularis* Labill. endemic to south-west Western Australia in swamps near Albany (Erickson 1968; Lowrie 1978). *Cephalotus* is traditionally related to the mainly extra-Australian families Saxifragaceae and Crassulaceae in the Rosidae: Saxifragales (summarised in Brummitt 1992). However, recent studies of the family's affinities by Albert *et al.* (1992) and Chase *et al.* (1993) using DNA sequencing found that its relationships were apparently closer to predominantly Australian or Gondwanan taxa such as the Tremandraceae, Eucryphia and Cunoniaceae in the higher Rosidae.

Seedling morphology and germination behaviour have long been known to have not only taxonomic (Vogel 1980) but ecological significance (Grubb 1977), with Gutterman (1994) observing that the degree of success at seedling establishment can determine the ultimate survival and fecundity of the adults. Establishment ecology is also related to features such as parental life-history strategy or adaptation to fire (Clifford 1981; Bell *et al.* 1993). Clifford (1981) deemed cryptocotylar germination to be in part an adaptation (at least in rainforests) to seedling grazing pressure by invertebrates, by protection of the cotlyedonary axillary buds inside the seed coat.

Germination patterns are are generally constant within genera (Clifford 1981), and Duke (1965) classified dicot germination types into phanerocotylar – the cotyledons emerge fully; and cryptocotylar, where they remain largely enclosed by the testa. Phanerocotyly always occurs with epigeal (above ground) germination and cryptocotyly is generally hypogeal (below ground), although Clifford (1984; 1991) listed several taxa with epigeal cryptocotyly. In addition, several plants with phanerocotylar germination then bury the plumule by elongation of the cotyledons (Jackson 1974). Similarly, in many monocots the hypocotyl is frequently elongated (Tillich 1995), resulting in some taxa such as the South African lily genus *Eriospermum* burying the plumule far below ground (Conran, unpubl. obs.)

Carnivorous plants have been the subject of a range of studies (summarised in Juniper *et al.* 1989) and there are reports on the seed structure and/or germination in the Droseraceae (e.g. Clifford 1984; Boesewinkel 1989; Conran *et al.* submitted), Nepenthaceae (Macfarlane 1908a) and Sarraceniaceae (Macfarlane 1908b). Similarly, the unusual pseudo-monocotyledonous seedlings of *Utricularia* (Lentibulariaceae) were detailed by Kondo *et al.* (1978).

Nevertheless, although the seeds and fruits of *C. follicularis* have been described by Corner (1976), and the germination conditions by Piliciauskas (1989), the detailed structure and germination characteristics are unreported. In particular, because there are a number of unusual features of the seedlings of *Cephalotus*, this present account details the morphology of its seedlings.

MATERIALS AND METHODS

Ripe seeds of *Cephalotus follicularis*, each still enclosed within their individual carpels, were sown on live *Sphagnum* in which the parent plant was growing. The 15 cm pot was watered from below by sitting it in a tray with 2 cm of rainwater and kept in an unheated glasshouse in Adelaide during summer 1991. Germination occurred in late autumn, and seedlings were collected at the 2–3 leaf stage and preserved in 70% ethanol. In addition, seedlings at a similar stage of development were observed in the field near Denmark in south-west Western Australia during late March 1994. Alcohol-cleared seedlings were rinsed in distilled water and then treated with a mixture of 1:1 phoroglucinol and 5M HCl, which is specific for lignin. Similarly, other cleared seedlings were immersed in I_2KI solution to test for the presence of starch in the hypocotyl or other seedling tissues.

RESULTS

The seedlings were phanerocotylar,

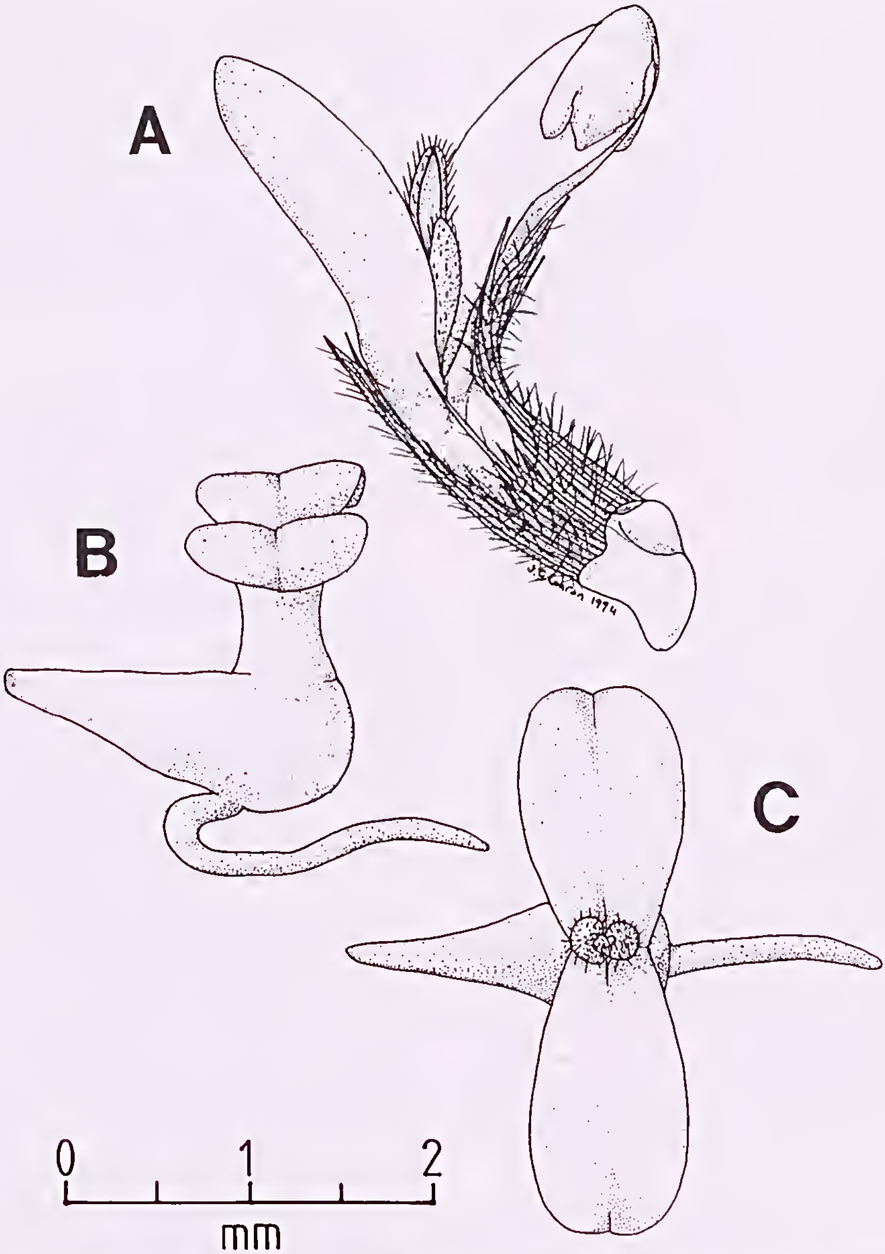

Figure 1. *Cephalotus follicularis* Labill. seedlings (all to indicated scale). A – seedling emerging from carpel follicle, with remnant seed coat on cotyledon apex. B – lateral view of seedling (follicle removed) showing radicle and extended hypocotyl. C – view of seedling from above showing expanded cotyledons and developing alternate first leaves (noncarnivorous).

with the cotyledons emerging from the carpel follicle which enclosed the seed (Figure 1A). Following expansion of the cotyledons, the remnants of the seed coat remained for some time on the apex of one of them. The cotyledons are obovate, glabrous and c. 2 mm long and 0.8–1.0 mm wide (Figure 1B,C). The first leaves are alternate and in both field and glasshouse grown plants, the first two leaves were non-carnivorous, although subsequent leaves may form pitchers. These first leaves were similar to the normal leaves of the plants. The radicle developed normally into the first root.

The unusual feature of the seedlings is that the hypocotyl base began to develop after germination, thickening to c. 1 mm diameter roughly 0.5 mm below the cotyledons and elongating up to a further 1.5 mm (Figure 1B–C) into the enclosing carpel remnant. This expansion occurred through the production of parenchymatous tissue which extended back into the carpel, filling the space. There was well developed and lignified xylem visible in the cleared, stained specimens extending through the hypocotyl from the cotyledon and leaf vascular traces to the radicle, but there was no lignified tissue or apparent vascularisation of the hypocotyl outgrowth. Neither the hypocotyl nor any other tissues contained starch.

DISCUSSION

In comparison with *Cephalotus*, germination in the other families of the Cunoniales such as the Cunoniaceae and Tremandraceae is phanerocotylar but otherwise unspecialised. The condition of hypocotylar development seems to be restricted to the Cephalotaceae, and possibly represents an ecological specialisation rather than phylogenetic trait. The absence of starch or of any vascularisation into the hypocotylar extension suggests that the region is not primarily a storage tissue, although there are storage compounds other than starches which might be present.

Cephalotus grows in moist *Sphagnum* swamps in south-west Western Australia, but as with most species of carnivorous plant, does not generally occur in standing water (Lowrie 1978). Although they grow in swamps, the plants are fire resistant, resprouting from a short rhizome. In addition, DeBuhr (1976) suggested from field observations that germination may be fire-induced. Because most carnivorous plants show very poor root development, especially as seedlings, they can have difficulty establishing quickly (Juniper *et al.* 1989), and Green (1967) noted for *Nepenthes* that the seed coat kept the seedling moist by capillary action. It is possible that the condition in *Cephalotus* is analagous. The tiny seed emerges from the follicle carrying the remnant testa on a cotyledon apex. Nevertheless, by then expanding the hypocotyl back into the much larger follicle remnant, the seedling may likewise obtain additional moisture via the hairs and ridges on the outside of the follicle. There may also be additional protection of the delicate seedling tissues from invertebrate grazers through partial enclosure, although further studies are needed to confirm this.

In conclusion, germination in the Cephalotaceae appears to have undergone specialisation. Because the seedlings are slow to develop the relatively few roots that the mature plants possess, the expansion of the hypocotyl back into the remnant follicle might serve as an additional moisture source via capillary action, and/or partial protection of the seedling from herbivores.

ACKNOWLEDGEMENTS

Leigh Garde Conran and José M. Facelli are thanked for comments on the manuscript.

REFERENCES

ALBERT, V.A., WILLIAMS, S.E. and CHASE, M.W. 1992. Carnivorous plants: Phylogeny and structural evolution. *Science* 257: 1491–1495.

BELL, D.T., PLUMMER, J.A. and TAYLOR, S.K. 1993. Seed germination ecology in south-western Western Australia. *Botanical Review* 59: 24–73.

BOESEWINKEL, F.D. 1989. Ovule and seed development in Droseraceae. *Acta Botanica Neerlandica* 38: 295–311.

BRUMMITT, R.K. 1992. *Vascular Plant Families and Genera.* (Royal Botanic Gardens: Kew.)

CHASE, M.W., SOLTIS, D.E., OLMSTEAD, R.G., MORGAN, D., LES, D.H., MISHLER, B.D., DUVALL, M.R., PRICE, R.A., HILLS, H.G., QUI, Y.-L., KRON, K.A., RETTIG, J.H., CONTI, E., PALMER, J.D., MANHART, J.R., SYSTMA, K.J., MICHAELS, H.J., KRESS, W.J., KAROL, K.G., CLARK, W.D., HEDRÉN, M., GAUT, B.S., JANSEN, R.K., KIM, K.-J., WIMPEE, C.F., SMITH, J.F.. FIJRNIER. G.R., STRAUSS, S.H., XIANG, Q., PLUNKETT, G.M., SOLTIS, P.S., SWENSEN, S.M., WILLIAMS, S.E., GADEK, P.A., QUINN, P.A., EGUIARTE, L.E., GOLENBERG, E., LEARN, G.H., JR., GRAHAM, S.W., BARRETT. S.C.H., DAYANANDAN, S. and ALBERT, V.A. 1993. Phylogenetics of seed plants: An analysis of nucleotide sequences from the plastid gene *rbc*L. *Annals of the Missouri Botanic Gardens* 80: 528–580.

CLIFFORD, H.T. 1981. Seedlings in the Australian flora. *Victorian Naturalist* 98: 75–79.

CLIFFORD, H.T. 1984. Cryptocotyly in Australian dicotyledons. *Flora Malesiana Bulletin* 37: 49–53.

CLIFFORD, H.T. 1991. Germination patterns in Dicotyledons. *Aliso* 13: 207–213.

CONRAN, J.G., JAUZDEMS, G. and HALLAM, N.D. submitted. Droseraceae leaf gland types, germination patterns and their taxonomic implications. *Botanical Journal of the Linnean Society.*

CORNER, E.J.H. 1976. *The Seeds of Dicotyledons Vol. I.* (Cambridge University Press: London.)

DE BUHR. L.E. 1976. Field notes on *Cephalotus follicularis* in Western Australia. *Carnivorous Plant Newsletter* 5: 8–9.

DUKE, J.A. 1965. Keys for the identification of seedlings of some prominent woody species in forest types of Puerto Rico. *Annals of the*

Missouri Botanical Garden 52: 315–350.

ERICKSON, R. 1968. *Plants of Prey*. Osborne Park, W.A.: Lamb.

GREEN, S. 1967. Notes on the distribution of *Nepenthes* species in Singapore. *Gardens Bulletin, Singapore* 22: 53–65.

GRUBB, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review* 52: 107–145.

GUTTERMAN, Y. 1994. Strategies of seed dispersal and germination in plants inhabiting deserts. *Botanical Review* 60(4): 373–425.

JACKSON, G. 1974. Cryptogeal germination and other seedling adaptations to the burning of vegetation in savannah regions: The origin of the pyrophytic habit. *New Phytologist* 73: 771–780.

JUNIPER, B.E., ROBINS, R.J. and JOEL, D.M. 1989. *Carnivorous Plants*. Academic Press: London.

KONDO, K., SEGAWA, M. and NEHIRA, K. 1978. Anatomical studies on seeds and seedlings of some *Utricularia* (Lentibu-lariaceae). *Brittonia* 30: 89–95.

LOWRIE, A. 1978. *Cephalotus* hunting in the deep S.W. of Australia. *Carnivorous Plant Newsletter* 7: 119–121.

MACFARLANE, J.M. 1908a. Nepenthaceae. *In* A. Engler (ed. *Das Pflanzenreich*. pp. 1–92. Engelmann: Leipzig.

MACFARLANE, J.M. 1908b. Sarraceniaceae. *In* A. Engler (ed. *Das Pflanzenreich*. pp. 1–39. Engelmann: Leipzig.

PILICIAUSKAS, E. 1989. *Cephalotus follicularis* and how to grow them from seed. *Victorian Carnivorous Plant Society Newsletter* 6(3): 12–15.

TILLICH, H.-J. 1995. Seedlings and Systematics in Monocotyledons. *In* P.J. Rudall *et al.* eds) *Monocotyledons: Systematics and Evolution*. pp. 303–352. Royal Botanic Gardens, Kew: London.

VOGEL, E.F.d. 1980. Morphological types in dicot seedlings with reference to their origin. *Bulletin de la Société Botanique de France, 126 Actual Botanique* 3: 173–182.